

THE ANNALS

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[SIXTH SERIES.]

“..... per litora spargite muscum,
Naiades, et circum vitreos considite fontes:
Pollice virgineo teneros hic carpite flores:
Floribus et pictum, divæ, replete canistrum.
At vos, o Nymphæ Craterides, ite sub undas;
Ite, recurvato variata corallia trunco
Vellite muscosis e rupibus, et mihi conchas
Ferte, Deæ pelagi, et pingui conchylia succo.”
N. Parthenii Giannettasii Rel. 1.

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I.—*On the Structure and Affinities of the Genus Parkeria, Carp.* By H. ALLEYNE NICHOLSON, M.D., D.Sc., Regius Professor of Natural History in the University of Aberdeen.

[Plate III.]

THE genus *Parkeria* was originally described by Dr. W. B. Carpenter (Phil. Trans. vol. clix. p. 721, 1870), and was regarded by this eminent authority as belonging to the arenaceous Foraminifera. At a later date the structure of the genus was investigated by Mr. Carter (Ann. & Mag. Nat. Hist. ser. 4, vol. xvii. p. 208, 1876, and vol. xix. p. 55, 1877), who came to the conclusion that the skeleton was not arenaceous in its composition, and that the genus was properly referable to the Hydractiniidæ. Mr. Carter's views have, in the main, been accepted by subsequent writers, such as Steinmann ('Palæontographica,' 1878, p. 118) and Zittel ('Handbuch der Palæontologie,' Bd. i. p. 283, 1879).

The purpose of the present communication is not so much that of entering into a critical examination of the views of previous observers as of recording the results of an entirely independent investigation into the structure of *Parkeria*. The observations and conclusions of both Dr. Carpenter and

Mr. Carter were based essentially upon specimens of *Parkeria* in one state of preservation, viz. specimens in which the chambers are non-infiltrated and the skeleton largely composed of phosphate of lime. The beautiful illustrations which accompany Dr. Carpenter's memoir were similarly derived mainly from specimens in the above condition of mineralization. This condition was regarded by Dr. Carpenter as being the one most nearly representing the original constitution of the fossil, whereas Mr. Carter recognized that it was secondary and the result of changes produced during the process of fossilization or at some subsequent period. The correctness of Mr. Carter's conclusion on this point does not, in my opinion, admit of reasonable doubt; and I propose in what follows to briefly describe the structure of *Parkeria* as exhibited by what I regard as normal examples of the genus, viz. examples in which the skeleton is composed of non-crystalline carbonate of lime and the chambers are infiltrated with calcite. Specimens in this condition of preservation are by no means uncommon; the phenomena which they present differ in no respect from those shown by similarly preserved examples of other calcareous fossils, such as corals, Polyzoa, Stromatoporoids, &c.; and their internal structure is so admirably preserved that they can be readily studied by means of thin sections. For much of the material with which I have worked I am indebted to the generosity of my friend Prof. T. M'Kenny Hughes, who was good enough to present to me a large series of specimens in all states of preservation. I have also to express my gratitude to Dr. P. Herbert Carpenter, who furnished me with the opportunity of examining the beautiful and instructive series of preparations of *Parkeria* upon which Dr. W. B. Carpenter had based his original memoir. Lastly, I have to thank Dr. John Millar for the free use of a large and interesting series of thin sections of *Parkeria*. My observations, however, are in the main founded upon an extensive series of slides which I have prepared myself.

1. *General Form and Mode of Growth.*

The ordinary form of *Parkeria* (*P. spherica*) presents itself, as is well known, in the shape of spherical bodies, which vary in diameter from less than half an inch to about two inches. The surface in unworn specimens exhibits rounded or elongated elevations, separated by intervening depressions, or, in other instances, may present an alveolar or honey-combed aspect. Rough fractures show that the skeleton is composed of numerous cylindrical columns ("radial pillars"),

which pass in a radiating manner from the centre to the circumference of the fossil, and are united at more or less regular intervals by imperfect concentric layers, which are separated from one another by concentrically disposed interspaces ("chamberlets").

As regards the mode of growth, most specimens must have been entirely free in the adult condition, since the entire surface is covered equally with the ends of the radial columns. Some examples, however, are pierced by a central cylindrical canal, as if they had grown upon some such body as the stalk of a Crinoid, which had been subsequently dissolved out. In other cases there is a similar central canal, but this does not extend more than halfway through the fossil. A similar complete or incomplete central perforation is common in the genus *Porosphaera*, Steinm., though my examination of this latter genus would lead me to conclude that it is in no way related to *Parkeria*. In most of the examples of *Parkeria* which I have examined, I have been unable to detect in the centre of the fossil any foreign body round which the organism may have grown. In this respect most examples resemble the singular fossil which I have recently described as *Mitcheldeania gregaria*. In some cases, however, the innermost or primordial layer of *Parkeria* has unquestionably been attached to the exterior of a foreign body, which appears generally to have been the shell of a small Nautilus or Ammonite. I have figured (Pl. III. fig. 6) a vertical section across the centre of such a specimen, showing the chambered Cephalopod round which the *Parkeria* has grown in successive concentric layers. It does not appear to me to admit of doubt that the chambered "nucleus" ascribed to *Parkeria* by Dr. W. B. Carpenter is really a foreign body of the above nature.

2. The Chemical Constitution of the Skeleton.

If any large series of specimens of *Parkeria* be examined, it will be found that different examples present great differences as regards the mineral nature and composition of the skeleton. The following are the principal variations which may be recognized in this respect:—

(a) In a certain proportion of specimens the skeleton is composed of carbonate of lime and the chambers of the fossil are occupied by calcite or by an infilling of the matrix in which the fossil was originally imbedded. The skeleton-fibre in these specimens is not in the condition of ordinary calcite, but is composed of subcrystalline granules of carbonate of lime.

(b) In a second group of specimens the skeleton is more or less extensively composed of phosphate of lime, and the chambers of the fossil may be occupied, throughout or in part, by phosphatic infilling. The greater proportion of the specimens which I have examined are in this condition; but the extent to which the skeleton is phosphatic varies greatly. In some examples the chambers of the fossil are filled throughout with phosphatic material, and the whole skeleton seems to be more or less largely made up of phosphate of lime. Even in such specimens, however, a certain amount of carbonate of lime is present in the skeleton, since the application of a drop of acid to a thin section of an apparently altogether phosphatic specimen is followed by an evolution of carbon dioxide. In most of the specimens belonging to this group, however, it is only *part* of the skeleton which is in the condition of phosphate of lime, and the remainder is in the condition of carbonate of lime. In such specimens it is invariably the *outer* portion of the specimen, for a zone of greater or less depth, which is phosphatic and has its chambers filled with phosphatic material, while the *inner* or central part of the specimen is composed of carbonate of lime and has its chambers filled with calcite.

(c) In a third group of specimens the skeleton is more or less largely composed of phosphate of lime and the central portion of the fossil, or the whole of it, has its chambers empty and non-infiltrated.

(d) In a fourth group of specimens the chambers of the fossil are infiltrated with silica. I have never seen an example in this condition of preservation; but such a specimen is stated by Dr. W. B. Carpenter to exist in the Museum of Practical Geology in Jermyn Street. The condition must, however, be one of great rarity.

The question now arises, What was the original composition of the skeleton of *Parkeria*? Dr. W. B. Carpenter regarded the specimens of the third of the above-mentioned groups as those least altered from their original constitution. He therefore considered that the skeleton was composed of a small proportion of sand-grains cemented together by a mixture of phosphate and carbonate of lime. Mr. Carter, on the other hand, regarded the phosphatic condition of the skeleton as of secondary origin and as being due to mineralization subsequent to fossilization. He appears to think that the skeleton may have been originally chitinous in nature, and that the chitine may have been replaced during fossilization by calcespar, which in turn might be more or less largely replaced at a later stage by phosphate of lime. My own view

is that the skeleton of *Parkeria* was composed originally of carbonate of lime, and that phosphatization, when it has occurred at all, has been the result of secondary processes which have operated subsequently to fossilization. The arguments for regarding the phosphatic condition of the skeleton as superinduced and not original may be briefly summed up as follows:—

1. The phosphatization of calcareous organisms is a well-known and readily intelligible phenomenon. Thus all kinds of calcareous fossils in phosphatic deposits (as in the Greensand near Cambridge) are liable to have their carbonate of lime more or less extensively replaced by phosphate of lime.

2. On the other hand, if we suppose an originally phosphatic organism to have its phosphate of lime replaced by carbonate of lime, then the latter mineral would certainly appear in the form of crystalline calcite. This is not the case, however, with the purely calcareous examples of *Parkeria*, the skeleton-fibre of which is composed of *granules* of carbonate of lime and not of definite *crystals*. Mr. Carter has described a specimen in which the skeleton-fibre is composed of calespar; but I have never personally met with a similar example, and such a condition must be regarded as the result of some secondary change.

3. In all those specimens of *Parkeria* which are partly phosphatic while parts are in the condition of carbonate of lime, it is invariably the *exterior* parts—which, necessarily, are those most exposed to chemical actions originating *ab extra*—which are phosphatic, while the internal and central portions are those which are calcareous. Moreover, even in the most highly phosphatic portions of such specimens, effervescence is produced by weak acids, showing that the original carbonate of lime has not been wholly removed or replaced.

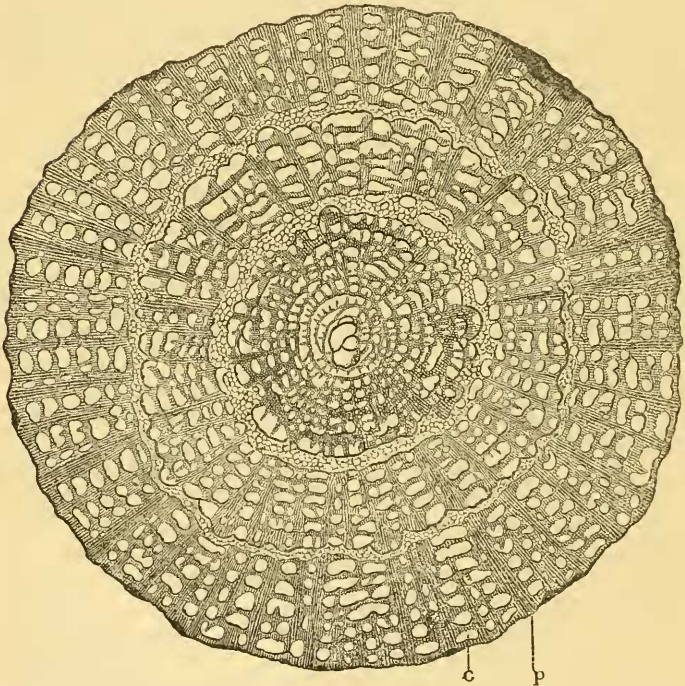
4. Thin sections of phosphatized specimens, or of the phosphatized parts of a specimen, show a more or less imperfect preservation of the minute structure of the skeleton. On the other hand, in specimens in which the skeleton is composed wholly of carbonate of lime the minute structure is exquisitely preserved.

Upon the whole, then, I cannot doubt that the skeleton of *Parkeria*, like that of the Stromatoporoids, was originally composed of carbonate of lime. The granules which compose the skeleton-fibre are not, however, infinitesimally minute, but are, on the contrary, of considerable size and of a sub-crystalline character. A closely similar composition of the skeleton out of large subcrystalline granules is seen in *Hydractinia circumvestiens*, S. V. Wood, and, very conspicuously,

in certain recent species of *Allopora*. In the phosphatized specimens of *Parkeria* the original granules of carbonate of lime have been replaced by granules of phosphate of lime; and if the specimen is non-infiltrated, *i. e.* has its chambers empty, the skeleton-fibre then assumes a peculiar "sandy" aspect. I have, however, failed to find in decalcified sections of any of the specimens which I have examined any sand-grains properly so-called; and I am therefore led to conclude that they did not exist, since it cannot be supposed that grains of quartz should have been replaced during fossilization by grains of phosphate or carbonate of lime.

3. *Minute Structure of the Skeleton.*

The skeleton of *Parkeria* consists of radiating columns ("radial pillars"), united by concentrically disposed lamellæ,



Vertical section across the centre of a specimen of *Parkeria*, enlarged twice. *p*, one of the radial pillars; *c*, one of the chamberlets.

which are separated by interspaces broken up into irregular "chamberlets" (see woodcut). One of the most remarkable points about *Parkeria* is the structure of the tissue which composes the radial pillars and concentric lamellæ. The nature of this tissue can be admirably studied in thin sections of calcareous examples of *Parkeria* (Pl. III. figs. 1-4), which show that it is composed of innumerable, minute, cylindrical or polygonal tubuli, which have a radial disposition and are united to one another by their walls. The walls of the tubuli are porous, thus allowing of a free communication between the cavities of adjacent tubuli. Vertical sections (Pl. III. figs. 2 and 4) show that the tubuli are vertical to the surface in the axes of the radial pillars, but that they become oblique to the surface as they proceed upwards. Hence each individual tubule has a proportionately short vertical course, beginning in the axis of the pillar and then gradually bending outwards so as to open obliquely on the circumference of the pillar. In cross sections of the pillars (Pl. III. figs. 1 and 3) the tubuli in the centre of the pillars are cut at right angles to their course and therefore present themselves as a polygonal network, like that of a Monticuliporoid. On the other hand, the tubuli in the peripheral portions of a cross section through a pillar are necessarily cut more or less obliquely, and their mouths are shown at the actual circumference of such a section. In the concentric lamellæ which connect contiguous pillars the tubuli are necessarily short; they originate from the calcareous membrane which forms the inferior surface of the lamella, and they open by minute apertures superiorly either into the cavities of the "chamberlets" or, in the case of the last-formed lamella, upon the outer surface of the cœnosteum.

The diameter of the tubuli composing the general cancellated tissue of *Parkeria* is about $\frac{1}{20}$ millim. The tubuli exhibit nothing of the nature of radiating septa, nor do they possess any "tabulæ" or transverse internal partitions. Owing to the fact that the tubuli are slightly flexuous, and owing also to their very minute size, longitudinal sections rarely divide a tubule in a single plane, but pass from side to side of its middle line, allowing the porous wall of the tubule to be seen at intervals, or here and there actually cutting the wall. Hence in longitudinal sections (Pl. III. figs. 2 and 4) there is often an appearance of tabulæ; but this appearance is due to the cause just mentioned. In the same way, sections which cut the tubules obliquely give the appearance not of proper tubes, but of rows of elongated polygonal cells. The general cancellated tissue of *Parkeria* may be regarded as

cœnosarcal in its origin, and it may be compared with the canaliculated cœnosarcal tissue of *Distichopora*, *Allopora*, *Pliobothrus*, &c., or with the clathrate cœnosarcal tissue of the *Hydractiniidæ*.

While the main mass of the skeleton of *Parkeria* is composed of the finely tubulated tissue above described, a coarser kind of cancellated tissue is commonly developed at particular points in the skeleton. The tissue in question (Pl. III. fig. 5) consists of wide, irregular, intercommunicating tubuli or elongated cells, united by a coarse reticulated tissue; and it is usually developed periodically in thin concentric layers, which separate thick strata of the ordinary skeletal tissue (see woodcut, p. 6). In small specimens it may not be developed at all, or there may be only a single external layer of it; but in large specimens there may be two or three successive layers in a section passing from the centre to the circumference. Sometimes also a similar tissue may occupy parts of the centre of a radial pillar. I am disposed to connect the periodic production of this coarse trabecular tissue, with its large vesicles, with the periodic development of reproductive zooids, and to compare it with the periodic production of "ampullæ" in the *Stylasterids*.

4. The Zooidal Tubes.

Traversing the general tubulated tissue of the radial pillars in *Parkeria* we find a larger or smaller number of comparatively wide circular or oval tubes, which have an average diameter of about $\frac{2}{3}$ of a millimetre. Owing to their being slightly oblique instead of accurately vertical to the surface, and owing also to the shortness of each individual tube, these structures are often badly exhibited in longitudinal sections of *Parkeria*. On the other hand, they are regularly and easily recognizable in tangential sections of the cœnosteum (Pl. III. figs. 1 and 3, *t*). These wide tubes vary in number in different specimens, but they are invariably present. They have no radiating septa, nor, so far as I have seen, transverse tabulæ. They open by rounded apertures upon the surface of the fossil or into the chamberlets—each successive concentric row of chamberlets having at one time formed the surface of the cœnosteum. I regard these large tubes as having contained zooids, and as corresponding therefore to the gastropores and dactylopores of the *Hydrocorallines*.

5. The Chamberlets and Concentric Lamellæ.

The first-formed layer of *Parkeria* has the form of a thin

calcareous membrane, which was probably always at first attached by its lower surface to some foreign body, such as a fragment of shell, though this latter seems to have been commonly absorbed in process of growth. The upper or free surface of the primordial lamina supports a layer of the characteristic tubulated tissue of *Parkeria*, which is prolonged upwards at small intervals into long pointed spines. This condition can be studied in vertical sections traversing the centre of the skeleton, and at this stage of its existence the organism must have presented a close resemblance to the crust of *Hydractinia echinata*, allowing for the fact that the cœnosteum is calcareous and not horny. In the further progress of growth the spines or primordial radial pillars throw out from their summits lateral outgrowths, which coalesce with one another more or less completely, and thus give rise to a second lamina, separated from the original one by an intervening space. This second lamina agrees with the first in having a calcareous membrane below and in being composed of tubulated tissue prolonged upwards into spines, which are mostly radial continuations of the primitive spines. The interspace between the first and second lamina is necessarily crossed by the primitive radial pillars, and hence appears in section as if broken up into separate "chamberlets" (Pl. III. fig. 6). As development proceeds the spines of the second series produce again a third lamella, thus giving rise to a second series of chamberlets; and so the process goes on till the organism has attained its full growth. The later lamellæ are generally thicker than the earlier ones and the rows of chamberlets proportionately more contracted (woodcut, p. 6); but there is no reason to think that the former are produced in any way differently from the earlier ones. After a certain number of lamellæ, with their corresponding rows of chamberlets, have been formed, it is common to find that a thin concentric layer of coarse cancellated tissue is produced, this possibly representing, as before suggested, a stage in the life of the organism in which reproductive zooids were developed. Then the ordinary lamellæ and spines are again formed, and we have a new series of concentric lamellæ and chamberlets. It is also not uncommon to find that growth is at first unilateral, the first two or three lamellæ being on one side only of the primordial crust, while the later lamellæ form complete concentric envelopes round the first-formed portion of the organism. It follows from the above account of the mode of development of the skeleton in *Parkeria* that each successive tier of chamberlets necessarily represents what was at one time the surface of the organism.

Bearing the above in mind, it is easy to understand the phenomena presented by sections of *Parkeria* vertical to the surface (woodcut, p. 6, and Pl. III. figs. 2 and 4). All such sections exhibit the radial pillars, the concentric lamellæ, and the concentric rows of chamberlets; and there is no difficulty in the recognition of the nature and mode of origin of these structures, if the plane of the sections corresponds accurately with the direction of the radial pillars. Sections tangential to the surface are not quite so easy of interpretation, though they present no special difficulties. Such sections differ according as the plane of the section corresponds with that of one of the concentric lamellæ or with a row of chamberlets. As the lamellæ are curved, an ordinary tangential section (Pl. III. figs. 1 and 3) passes partly through one of the concentric lamellæ and partly through a tier of chamberlets. Hence such a section usually shows more or less clearly the cut ends of the radial pillars (*p*) connected by a reticulated tissue representing the transversely divided tubuli of the concentric lamellæ. Here and there we also see irregular spaces (*c*), which represent the chamberlets opened from above. In places where the section corresponds with a row of chamberlets, we see simply the cut ends of the radial pillars. In either case, tangential sections clearly exhibit the transversely-divided zoöidal tubes (*t*).

6. Relation to Recent Organisms.

With regard to the systematic position of *Parkeria*, there can be little hesitation, in the light of our present knowledge, in accepting Mr. Carter's reference of the genus to the Hydrozoa. All the known facts as to the chemical constitution, mode of growth, and general structure of the cœnosteum, no less than the minute structure of the skeleton-fibre, point unequivocally in this direction. With regard to the precise place which *Parkeria* should occupy in the series of the Hydrozoa, it may be regarded as intermediate between the Hydrocorallines and the Hydractiniidæ, but with nearer relationships to the latter than to the former. In the minute structure of the skeletal tissue *Parkeria* most closely resembles the Hydrocorallines; but in the general arrangement of its parts, and more particularly in its mode of growth by the production of successive concentric lamellæ separated by rows of chamberlets, it approaches most nearly to the Hydractiniidæ, with which group the genus may in the meanwhile be ranked.

7. Relations to Extinct Organisms.

There are various extinct organisms which have, or have been supposed to have, relationships with *Parkeria* which may be briefly glanced at here. Foremost amongst these may be placed the singular spheroidal fossils from the Triassic rocks of Kashmir, which Prof. P. Martin Duncan described under the family name of the *Syringosphaeridæ* ('Scientific Results of the Second Yarkand Mission,' 1879). By the great kindness of Mr. Medlicott, the Director of the Geological Survey of India, and of Dr. Henry Woodward, I have been supplied with specimens of *Syringosphaera*, of which I have made a careful examination by means of thin sections. In their general aspect the fossils of the genus *Syringosphaera* present an exceedingly close resemblance to *Parkeria*, with which they also agree in the possession of a tubulated cœnosteal tissue. On the other hand, the cœnosteum in *Syringosphaera* does not increase by the formation of successive concentric lamellæ with intervening rows of chamberlets, and I have been able to demonstrate the presence of well-marked zoöidal tubes ("gastropores") occupied by reticulate styles or columellæ. I shall be able, in fact, to show that the genus *Syringosphaera*, Duncan, is referable to the Hydrocorallines and is nearly related to the recent genera *Allopora* and *Sporadopora*; but I need not enter further into this point on the present occasion, as I purpose treating of the genus more fully in a separate memoir.

The genus *Porosphaera*, Steinmann, was referred by its author ('Palæontographica,' N. F. Bd. iii.) to the Hydrozoa, and was looked upon as related to *Parkeria*, a view which had previously been put forward by Mr. Carter (Ann. & Mag. Nat. Hist. 1877). I have prepared and examined a number of thin sections of *Porosphaera globularis*, Phill. sp., from the White Chalk of Britain, and do not feel able to coincide in the above view. Without expressing any dogmatic opinion on the subject, I am disposed to think that *Porosphaera* will be found to be truly referable to the group of the Lithistid sponges, and to be related to the genus *Hindia*, Dunc. It is, at any rate, certain that the genus has no special relationship with *Parkeria*, and the minute structure of its skeleton does not resemble that of any Hydrozoön with which I am acquainted. *Bradya tergestina* of Stache is unknown to me, and I am unable to express any opinion as to its affinities.

The genus *Loftusia*, H. B. Brady (Phil. Trans. 1869), has been regarded by Steinmann, Carter, and others as likewise referable to the Hydrozoa, and as more or less nearly related

to *Parkeria*. I have only had the opportunity of studying *Loftusia* through the medium of thin sections; but I am quite satisfied that its resemblances to *Parkeria* are superficial, and are not indicative of any real affinity. I do not recognize in the structure of *Loftusia* any thing distinctively Hydrozoal, whilst it possesses structural features, apart from its spiral mode of growth, that are strongly Foraminiferal. Upon the whole, therefore, the present evidence seems to me to fully warrant Mr. Brady's reference of the genus *Loftusia* to the arenaceous Foraminifera.

The curious spheroidal fossils which constitute the genus *Mitcheldeania*, Wethered, present some striking resemblances to *Parkeria*. The minute structure of the skeleton of the former is, however, in essential respects different from that of the latter, while the chamberlets which are so characteristic of *Parkeria* are wanting in *Mitcheldeania*. As I have, however, treated fully of the structure of the genus *Mitcheldeania* in another communication (Geol. Mag., Jan. 1888), I need not enter here into a further consideration of its characters and relationships.

Lastly, there are unquestionable points of resemblance, as well as marked points of difference, between *Parkeria* and the great Hydrozoal group of the Stromatoporoids. No Stromatoporoid, however, possesses the peculiar tubulated cœnosteal tissue of *Parkeria*. The nearest approach to this is seen in the genera *Stromatopora*, Goldf., *Stromatoporella*, Nich., and *Parallelopora*, Barg.; but the skeleton-fibre in these genera is vesicular rather than tubulated, and the general structure of the skeleton is fundamentally different from that of *Parkeria*. The genus *Labechia*, E. & H., which might in some points be compared with *Parkeria*, is even more widely removed from it than are the above genera as regards the internal structure of the skeleton.

EXPLANATION OF PLATE III.

- Fig. 1.* Tangential section of *Parkeria spherica*, enlarged about ten times. *p*, one of the radial pillars transversely divided; *t*, one of the zoöidal tubes; *c*, one of the chamberlets.
- Fig. 2.* Vertical section of the same, similarly enlarged. *p*, one of the radial pillars; *c*, one of the chamberlets; *l*, calcareous lamina supporting one of the concentric lamellæ.
- Fig. 3.* Tangential section of *Parkeria*, enlarged about twenty times; the letters as before.
- Fig. 4.* Vertical section of the same, similarly enlarged; letters as before.
- Fig. 5.* Tangential section through one of the periodically-formed layers of coarse cancellated tissue, enlarged about twenty times.
- Fig. 6.* Central portion of a vertical median section of a specimen of *Parkeria* growing upon a chambered Cephalopod, enlarged about ten times.